**Title:** Spatial density and habitat associations of Atlantic Cod on the Northeastern US Continental Shelf

**Authors:** Katelynn M. Lankowicz a, Jonathan H. Grabowski b, Graham Sherwood a, Lisa Kerr a, c

a. Gulf of Maine Research Institute, Portland, ME, USA

b. Northeastern University, Marine Science Center, Nahant, MA, USA

c. University of Maine, School of Marine Sciences, Orono, ME, USA

**Corresponding author:** K. Lankowicz, klankowicz@gmri.org

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**1 Abstract**

The spatial distribution of the Atlantic cod (*Gadus morhua*) population is shaped by a suite of habitat and oceanographic variables. Additional complexity is added by differences in environmental preferences between life-history phases and biological stocks. Multiple bottom trawl survey programs are used to assess groundfish abundance in the Northeastern US Continental Shelf (NEUS), but bottom trawls have reduced efficiency in complex bottom habitats that are highly suitable for Atlantic cod. Modeling cod spatial density from a combination of survey methods across multiple habitat types would help to bridge this gap. In this study, Vector Autoregressive Spatio-Temporal (VAST) models were used to combine data from survey programs using bottom trawls, bottom longlines, and video trawls to hindcast seasonal spatial density of three size classes of cod within the NEUS from 1982 to 2021. Bottom habitat characteristics (sediment type, rugosity, and depth), bottom water temperature, and basin-averaged climate indices (North Atlantic Oscillation and Atlantic Multidecadal Oscillation) were included as covariates to improve predictions of population density. Indices of abundance, habitat associations, center of gravity, and other spatial dynamic metrics were generated from the results. Indices of abundance and spatial dynamic metrics were further separated into the four spatially separate biological stock areas of the cod population. Abundance of all size classes generally decreased within all stock areas. Depth and bottom temperature were strongly associated with cod spatial density. The center of gravity for medium (40-70cm) and large (>70cm) cod moved northeast in spring and north in fall. Large cod had a sharp decline in spatial area utilized, particularly in the spring. Small (<40cm) cod populations moved north in fall and had high variability with no clear trend in spring. As distributions of most cod stocks shift north and offshore, the availability of habitat with suitable depth and temperature will likely be reduced, further endangering the recovery of the cod population. Improving our understanding of cod habitat preferences and variation in spatial density among the biologically distinct stocks will be important for future management efforts.

**Keywords:** Atlantic cod, vector autoregressive spatio-temporal model, spatial density, habitat

**2 Introduction**

Atlantic cod (*Gadus morhua*) are an ecologically, economically, and culturally critical part of New England’s fishing industry. However, the groundfish fishery has been under a disaster declaration since 2012 due to historically low abundance and rapidly declining stocks. Atlantic cod population assessments and management efforts are informed by a suite of bottom trawl surveys, perhaps most notably by the Northeast Fisheries Science Center’s (NEFSC) twice-annual bottom trawl survey. This survey has been an important tool to assess groundfish stocks from Cape Hatteras, NC to Nova Scotia since the early 1960s. However, bottom trawl surveys like the NEFSC bottom trawl are known to have reduced efficiency over complex bottom habitats with high bathymetric relief or hard substrate, such as cobble fields or rocky ledges (McElroy et al. 2019; Grabowski et al. 2020). Most bottom trawl survey programs have low sampling effort within shallow or complex habitat areas due to risks to the equipment and will instead focus on sampling in areas deeper than 18m and with soft and smooth bottom habitats (Johnston and Sosebee 2014).

The limited survey information within complex bottom habitats is concerning to fishing industry stakeholders, fisheries scientists, and fisheries managers alike. Habitat complexity likely interacts with catchability, thereby making it difficult to determine if differences in catch between habitats are truly reflective of relative abundance (Peterson and Black 1994; Grabowski et al. 2020). The challenge this poses to assessments will vary with life history phases; several early life history phases of cod are known to be associated with complex bottom habitat areas and therefore are not likely to be sampled well by conventional bottom trawl methods. Age-0 and age-1+ juvenile cod have been found in higher densities over hard substrate or high-bathymetric relief areas, likely as a refuge from predation (Gotceitas and Brown 1993; Gotceitas et al. 1995; Gregory and Anderson 1997; Cote et al. 2004; Lough 2010; Grabowski et al. 2018; Linner and Chen 2022). Though conventional wisdom holds that adult cod prefer colder and deeper offshore waters, recent evidence indicates that shallow inshore areas support a wide range of cod by length (Dean et al. 2021). Industry stakeholders also have reported a relatively high density of large cod within inshore hard-bottom habitats of the western Gulf of Maine, possibly indicating a density-dependent reduction in large cod spatial distribution and altered availability to bottom trawl surveys (Grabowski et al. 2020; McElroy et al. 2021). Stakeholders’ observations of high cod density over complex bottom habitats have created the perception that cod abundance across most of the species' spatial range is much higher than what bottom trawl-informed assessments have suggested, which could strain relationships between scientists, managers, and stakeholders.

A further complication to assessing cod population spatial dynamics is the complicated spatial structure of its subpopulations. Since 1972, cod in US waters have been managed as two units: the Georges Bank and Gulf of Maine stocks (Serchuk and Wigley 1992). This structure may not have captured the biological structure of the cod population, leading to misinterpretations of the distribution of the magnitude and productivity of the population (Kerr et al. 2014; Zemeckis et al. 2014). Recent work by the Atlantic Cod Stock Structure Working Group has provided evidence that there are five biological cod stocks in US waters: a Georges Bank stock, a Southern New England stock, an Eastern Gulf of Maine Stock, a spring-spawning Western Gulf of Maine stock, and a winter-spawning Western Gulf of Maine and Cape Cod stock (McBride and Smedbol 2022). The former three stocks inhabit spatially separate areas, and the latter two stocks are sympatric with an area of overlap in the western Gulf of Maine. Each of these spatial areas has a unique composition of static spatial features (depth, bottom substrate) and dynamic environmental characteristics (seasonal water temperature) that are expected to influence the habitat use and productivity of the associated cod stock (Ames 2004; Zemeckis et al. 2014; Guan et al. 2017a; Dean et al. 2019; Linner and Chen 2022). Tracking the varying spatial dynamics and productivity of cod populations at spatially explicit and biologically relevant scales will be critical to developing useful management strategies (Kerr et al. 2014; Zemeckis et al. 2014; Dean et al. 2019; McBride and Smedbol 2022).

The objective of this study is to build a joint index of abundance and annual maps of spatial density for Atlantic cod for each of the stock areas using all relevant state and federal groundfish survey data. Available data includes inshore, offshore, smooth, and complex bottom habitats, and utilizes both bottom trawl and hook-and-line methods. Vector Autoregressive Spatio-Temporal (VAST) models were used to address this objective. VAST models estimate the spatial density of multiple categories of a target organism conditioned on density covariates and controlling for catchability covariates. These estimates of spatial density can then be used in the calculation of indices of abundance. The resulting spatially explicit combined indices could improve our understanding of cod spatial dynamics, habitat associations, and demographics, which in turn would benefit management efforts and help rectify opposing perceptions of cod population size.

**3 Methods**

**3.1 Survey Data**

Eleven surveys of groundfish abundance are currently available for use (Table 1). The combined spatial footprint of all surveys covers the waters of the continental shelf along the US coast from Lubec, Maine to Cape Hatteras, North Carolina. Temporal coverage spans from 1959 to 2022. These surveys utilize different vessels and methods, have variable spatial extents, are completed either annually or seasonally, and are of variable temporal length (as in, the number of years in which the survey has occurred). All surveys report the number of cod and total weight (kg) of cod caught per tow, and some surveys process all or a portion of the catch to provide further biological detail (individual length, weight, sex, age, etc.). Survey data needs to be cleaned, cut to chosen model spatial and temporal domains, and combined into a single dataset before the modeling process.

**3.1.1 Data cleaning and response variable**

To be considered in the model, survey data needed to have valid information for spatial location, sampling date, and number of cod caught, and valid size-identifying biological information for at least a portion of the catch. Cod caught in the surveys were separated into three classes, as it was expected that habitat utilization and spatial density would vary among size or age groups. Small fish were defined as shorter than 39.1 cm total length or less than 0.58 kg. Medium fish were between 39.1 and 70.2 cm, or between 0.58 and 3.44 kg. Large fish were longer than 70.2 cm or heavier than 3.44 kg. This size structure roughly matches ages 0-2 (pre-spawning), ages 2-5 (spawning), and ages 5+ (mature) cod (Zemeckis et al. 2014; Dean et al. 2019; Dean and Perretti 2022). This age structure represents the average across all years and all spatial areas of the model domains and may be slightly different among periods and locations (Dean and Perretti 2022). Fish unable to be assigned to a size category could not be used in the model. Because some fish had no associated individual weight information, biomass per size category could not be used as the model’s response variable. Instead, total abundance of each of the size classes was used as the response variable for each sampling event.

**3.2 VAST**

VAST models were used to estimate cod spatial density over time by size class and create joint indices of abundance using the cleaned groundfish survey data. VAST is a framework for implementing spatial delta-generalized linear mixed models (delta-GLMM) and can be manipulated to provide estimates for multiple categories of interest and spatial strata (Thorson and Barnett 2017; Thorson 2019). It is structured to utilize two linear predictors; the first linear predictor estimates encounter probability, and the second linear predictor estimates catch rates. Using notation from Thorson (2019), the first linear predictor can be represented as

1.

where is the encounter probability predictor for observation *i* for category at location and time . represents temporal variation for each category and time, represents spatial variation for each location and category, represents spatiotemporal variation for each location, category, and time, represents vessel effects for each vessel and category, and represents the effect of density covariates for each category and time. The second linear predictor is structured the same way but calculates the catch rate predictor. Both linear predictors incorporate fixed and random effects, and spatial and spatiotemporal variation are approximated as Gaussian Markov random fields (Thorson et al. 2015b; Thorson and Barnett 2017; Thorson 2019). As recommended by model developers for abundance-data models, a lognormal-Poisson distribution was chosen for the first linear predictor and an alternative “Poisson-link delta-model” was chosen for the second linear predictor.

Implementation of VAST models requires several structural and data inclusion decisions, as outlined in Thorson (2019). Decisions used in this effort will be discussed in the following subsections.

**3.2.1 Spatial domain, smoothing, resolution, and strata**

Though survey data coverage extends to Cape Hatteras, North Carolina, the southern edge of the Atlantic cod range likely does not reach this point. For this model, the spatial extent of interest will be American waters on the continental shelf from the northern edge of the Gulf of Maine through the mouth of the Chesapeake Bay (Fig. 1). This area was represented as a “2D mesh” built on a stochastic partial differential equation (SPDE) approximation to a Gaussian Markov Random Field with a Matérn correlation function. Geometric anisotropy (directional correlation) is expected in most marine ecosystems (Thorson et al. 2015a) and was therefore included as a fixed effect, though support for its inclusion was also assessed in the model selection process. Spatial variables are defined at a pre-determined number of knots, which are placed via k-means clustering of the data to minimize the average distance between knots and sampling locations. Sampling locations are expected to have spatial variables equal to the nearest knot, so in effect, the number of knots defines the spatial resolution of spatial density estimates. In this model, the number of knots was set to 200 and the average minimum distance between knot locations was 31.0 km. Later assessment of geostatistical range found that the distance with approximately 10% correlation was 112.8 km for the first linear predictor and 64.5 km for the second linear predictor, indicating that this number of knots provides sufficient spatial resolution.

Previous work by the Atlantic Cod Stock Structure Working Group has provided evidence that there are five biological cod stocks in US waters: a Georges Bank stock, a Southern New England stock, an Eastern Gulf of Maine Stock, a spring-spawning Western Gulf of Maine stock, and a winter-spawning Western Gulf of Maine and Cape Cod stock (McBride and Smedbol 2022). There is evidence that the complex spatial structure of these biological stocks affects both our understanding of cod spatial dynamics and management efforts (Zemeckis et al. 2014; Guan et al. 2017a; McBride and Smedbol 2022; Linner and Chen 2022) and so it is of interest to calculate metrics of spatial dynamics and indices of abundance for each spatial strata. Therefore, a custom extrapolation grid was built as a spatial domain for derived quantities, which had 2000 grid cells (approximately 25 km by 25 km) spread across four spatial strata. VAST later uses bilinear interpolation to calculate spatial density within each of these cells. The spatial strata represent the Eastern Gulf of Maine, Georges Bank, Southern New England, and combined winter- and spring-spawning Western Gulf of Maine stocks. The latter two stocks overlap substantially in space, supporting their treatment as a single spatial stratum. The model will also report results at a basin-wide scale, in which all strata are combined.

**3.2.2 Temporal domain and resolution**

The temporal domain of the model begins in 1982, when the adoption of the Interim Groundfish Plan shifted management strategies from regional quotas to minimum size and gear regulations. The last full year of data available at the time of modeling was 2021. Survey data from outside this temporal domain was not used in the model.

Many surveys considered by this modeling effort are conducted twice annually, in the spring and fall. This is a useful sampling design to track seasonal migrations; cod are expected to migrate inshore to spawn in the spring, move offshore to feeding areas in the summer and fall, and may move to deep offshore basins to overwinter (Zemeckis et al. 2017). Because it is supported both by data availability and the behavior of cod, time steps in the model were structured to represent the spring and fall seasons of each year in the time series. Therefore, though there are 40 years of data, there are 80 time steps. The spring season is March through August of any year *x*. Fall is September through December of year *x* and January and February of year *x*+1. This is to ensure that the fall season is temporally continuous, rather than interrupted by the defined spring period.

**3.2.3 Effort estimates**

VAST requires an effort estimate for each observation. For surveys using bottom trawl methods, area swept is a commonly reported effort measure. Area swept was reported, assumed, or calculated for the surveys included in this modeling effort as information was available (Table 1). Some bottom trawl surveys reported area swept for each tow, and this was therefore used as an effort estimate. Several surveys did not report the area swept for each tow but instead reported an average area swept based on gear mensuration and vessel distance. Typically, these surveys also validated that effort was within tolerance limits for acceptable tow duration and vessel speed to maintain similarity between tows. For these surveys, this average area swept was included as the estimated effort for each observation. Finally, a few surveys reported only optimal gear mensuration and intended distance towed. For these surveys, the estimated effort per tow was calculated as the intended distance covered by the tow multiplied by the optimal wing spread.

It is recommended that the area swept be set to 1 for sampling gears with an unknown effective area swept (Thorson 2019). Initially, the area swept for the bottom longline and Sentinel jigging surveys was set to 1. However, this created an issue of scaling and mixed units. Simple leave-one-out sensitivity tests were run to determine the influence of the bottom longline and Sentinel jigging surveys on the overall cod indices of abundance. Removing the Sentinel jigging survey had little impact on the modeled abundance of all three size classes of cod, so it was excluded from further analysis (Suppl. Fig. 1). Removing the bottom longline survey reduced the abundance of medium and large cod by up to 50% in some years and was therefore retained in further analyses. The description of the bottom longline motivation and methods in McElroy et al. (2019) states that it was developed to match the sampling effort of the NEFSC bottom trawl survey as closely as possible. For this reason, the average area swept of the NEFSC bottom trawl survey was used as the input for the area swept of the bottom longline survey.

**3.2.4 Spatial, temporal, and spatiotemporal effects**

Spatial, temporal, and spatiotemporal autocorrelation can be included in both linear predictors. A model selection process was used to justify the use of spatial and spatiotemporal random effects in the first and second linear predictors. The intercept for each linear predictor was defined as a fixed effect for each time step– this ensures independent estimates of abundance for each time step, which is most appropriate for creating abundance indices (Thorson 2019). A temporal correlation component was estimated for the spatiotemporal variation in both linear predictors. This is recommended for indices generated by multiple data sources that do not necessarily sample the same locations in every time step (Thorson 2019). Without this estimation, unrealistic “hot spots” may develop or be carried through the time series when this is inappropriate. Because the model includes data from surveys with varied sampling intensity, locations, and temporal scales, this is an important structuring decision. The use of temporal correlation for spatiotemporal variation can also help interpolate density in unsampled time steps (Thorson 2019).

**3.2.5 Vessel effects**

The random variation in catchability among levels of a grouping variable is referred to as “vessel effects” in the VAST model structure. VAST models covariation in vessel effects with a factor model, where variation in catchability between groups is a random effect. Each survey used in this modeling effort has its own set of sampling protocols and vessels, and these differences likely introduce variability in catchability. Therefore, vessel effects were included in this model. It is understood that multiple vessels were sometimes used to complete each survey, but most surveys did not specify the vessel used for each sampling event. Instead, we used the survey as the grouping variable rather than the vessel.

**3.2.6 Density Covariates**

VAST allows for the effects of both density and catchability covariates to be included in modeling efforts. Catchability covariates are processes that affect the ability to observe the target organism without necessarily affecting the distribution of the organism. Density covariates are processes that directly affect the distribution of the target organism, regardless of the ability to observe it. Both covariates affect the catch rate of the target organism, but only density covariates are used to predict target organism density within the spatial domain. Therefore, VAST “controls for” catchability covariates and “conditions on” density covariates. VAST is unable to distinguish whether potential covariates should be treated as catchability or density covariates; this must be decided with theoretical insight from an analyst. As mentioned previously, differences in sampling design were included as vessel effects, but explicit catchability covariates were not used. Several environmental variables were tested as potential density covariates. The final model only includes density covariates with significant impact, as determined by a model selection process that will be discussed later in this document.

**3.2.6.1 Environmental variables**

Depth is known to strongly influence the distribution and habitat use of Atlantic cod (Lough 2010; Guan et al. 2017b; Li et al. 2018; Linner and Chen 2022). Very few cod are found in waters deeper than 400 m, and the highest densities of cod are found in the range of 10-150 m (Lough 2010). Depth at all survey locations was interpolated from rasterized GEBCO 15 arc-second bathymetry and included as a potential density covariate.

There is evidence that cod habitat preferences include large-grain sediments like gravel, cobble, and boulders, making sediment type an important environmental covariate to consider when mapping spatial density (Gotceitas and Brown 1993; Gotceitas et al. 1995; Methratta and Link 2006; Lough 2010; Grabowski et al. 2018; Linner and Chen 2022). The spatial distribution of sediment types through the VAST model’s spatial domain was modeled by Brad Harris and Felipe Restrepo at Alaska Pacific University (Harris and Restrepo, pers. comm.). This model is an expansion on the New England Fishery Management Council Swept Area Seabed Impact (SASI) model, which used sediment observations from many sources to classify bottom habitat by sediment particle size (based on Wentworth 1922) and model spatial distribution of all classes of sediment with an unstructured Voronoi tessellation (Bachman et al. 2011, 2019). The sediment classes are based on Wentworth (1922): mud, sand, gravel, cobble, and rock (Table 2). The new model uses an ordinary kriging approach to interpolate the likelihood of finding any of the five sediment classes within the cells of a 1 km by 1 km resolution grid with the same spatial extent as the VAST model.

There is further evidence that cod prefer habitats with high bathymetric relief, like boulders and steep ledges (Gregory and Anderson 1997; Cote et al. 2004). Bathymetric relief was characterized by rugosity, which is a unitless measure of bottom vertical change over horizontal distance. Using methods outlined in Friedman et al. (2012), rugosity was calculated from the 15 arc-second rasterized bathymetry data over the VAST model’s spatial domain. Rugosity at each survey location was extracted from the resulting rugosity raster.

The previous density covariates are spatially dynamic but temporally stationary. Cod distribution is also known to be temporally dynamic, as cod have seasonal migrations that likely reflect shifting water temperatures (Lough 2010; Zemeckis et al. 2017; Li et al. 2018). Sea surface temperatures (SST) could affect spawning and recruitment success, and so were included as potential density covariates (Planque and Frédou 1999; Drinkwater 2005; Fogarty et al. 2008; Pershing et al. 2015; Klein et al. 2017). Though most surveys measured and reported SST for every observation, the empirical dataset includes many missing SST values. VAST cannot tolerate missing values in density covariates, and removing a large chunk of data was undesirable. Therefore, NOAA’s 1/4° spatial resolution daily Optimum Interpolation SST (OISST) data product was used to fill gaps. OISST daily rasters were pulled from NOAA data sources and SST was extracted at observation locations. OISST values were compared to field measurements, when available, and the two were found to be generally similar (Suppl. Fig. 2).

Bottom water temperatures are also expected to shape cod distribution and productivity (Drinkwater 2005; Methratta and Link 2006, 2007; Guan et al. 2017b). Bottom temperature data were provided by Du Pontavice et al. (2023). The bottom temperature within approximately 5-minute by 5-minute grid cells was calculated at a daily timestep for 1982 to 2020. Bottom temperature data were not modeled for 2021, the final year in the VAST model’s temporal domain. Bottom temperature data from 2020 were used to fill this gap, as it was assumed that bottom temperature trends would remain similar between sequential years. Further, the bottom temperature product did not extend to the inshore strata included in the model. To fix this issue, the bottom temperature was interpolated to the inshore strata using an ordinary kriging approach.

**3.2.6.2 Climate Indices**

Several climate indices have been demonstrated to have a spatially variable relationship to cod recruitment and abundance, as they are associated with spatially variable long-term warming (Pershing et al. 2015). For this model, North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO) index data were used as spatially static basin-wide climate indices and tested for inclusion in the final model. NAO is a measure of differences in atmospheric pressure at high and low latitudes of the North Atlantic and is expected to affect the intensity and location of wind patterns, heat transport, and moisture transport. AMO measures average anomalies of sea surface temperature in the North Atlantic basin. Data for both climate indices are publicly available in NOAA’s data repositories. NAO is calculated at a daily timestep, whereas AMO is calculated at a monthly timestep. Values for both climate indices were extracted for every survey observation at the best available temporal resolution.

**3.3 Model selection**

The model selection process was completed in two steps. The first step compared models with and without anisotropy and/ or spatial and spatiotemporal random effects in the first and second linear predictors. The second step was to compare models with all possible combinations of the nine density covariates. This follows the model selection process of Ng et al. (2021) and Gaichas et al. (2023).

Models were tested for different values in the Field Configuration settings (testing the use of spatial and spatiotemporal variation in the linear predictors), anisotropy, and overdispersion (Table 3). AIC was used to compare models and restricted maximum likelihood (REML) was used in model construction to make comparison via AIC possible (Zuur et al. 2009). The best model included anisotropy and spatial and spatiotemporal effects in both linear predictors.

Model naming conventions are as follows:

* “alleffectson” - anisotropy on, spatial and spatiotemporal random effects in both linear predictors
* “noaniso” - anisotropy off, spatial and spatiotemporal random effects in both linear predictors
* “noomeps2” - anisotropy and spatial and spatiotemporal effects in linear predictor 1
* “noomeps2\_noaniso” - anisotropy off, spatial and spatiotemporal effects in linear predictor 1
* “noomeps2\_noeps1” - anisotropy and spatial effects in linear predictor 1
* “noomeps2\_noeps1\_noaniso” - anisotropy off, spatial effects in linear predictor 1
* “noomeps12” - anisotropy on, no spatial or spatiotemporal effects
* “noomeps12\_noaniso” - anisotropy off, no spatial or spatiotemporal effects

Potential density covariates were tested for collinearity. High correlations were found between two pairs: cobble and rock sediment probability, and OISST and bottom temperature. The probability of rock sediment type and OISST were removed as covariates. Rock sediment probability was removed as grab and coring samplers (the bulk of sediment samples that make up the dataset) are unlikely to sample large-grain sediments like boulders effectively, and so the lower data quality that feeds this model will inevitably result in a lower-quality and less-reliable model of large-grain sediment distribution (Bachman et al. 2011). For the second pair, OISST was removed as it was expected that as groundfish, cod distribution would be more directly affected by bottom temperature than sea surface temperature. Once these two collinear relationships were addressed, the remainder of density covariates were not correlated and therefore were tested for inclusion in the final model.

Density covariates were selected for inclusion into the final model by running a subset of the original observation data (the last 5 years of NEFSC bottom trawl data) with all possible combinations of variables as spatial density inputs (Table 4). The four sediment likelihood variables (cobble, gravel, sand, and mud) were never separated, as the entire suite of sediment probabilities is needed to characterize bottom habitat. Models were then compared using AIC. Maximum likelihood was used to calculate AIC, as the spatial and spatiotemporal random effects did not change between models. The model with the lowest AIC was the model that included spatial density terms for all potential covariates.

Model naming conventions are as follows:

* “seds” - all sediment likelihood variables (cobble, gravel, sand, and mud)
* “rugos” - rugosity
* “bathy” - bathymetry
* “bottom” - bottom temperature
* “nao” - daily North Atlantic Oscillation index
* “amo” - monthly North Atlantic Oscillation index

**3.4 Final model**

After the model selection process, the best model included anisotropy, spatial, and spatiotemporal random effects in both linear predictors and density covariates for four classes of sediment types, rugosity, bathymetry, bottom temperature, NAO index, and AMO index. The final model was also run with bias correction turned on, which uses the “epsilon method” to ensure that the mean and variation of generated indices of abundance are not biased due to their transformation by a nonlinear function in the modeling process (Thorson and Kristensen 2016).

**4 Results**

**4.1 Spring Index**

Large cod had the lowest abundance within the study area of all three size classes, and abundance for this group decreased over time. This result held for indices calculated within each of the four stock areas as well. Large cod were most abundant in the Georges Bank stock area. The center of gravity for large cod tended to be within the Georges Bank stock area and shifted slightly offshore over the time series. The effective area occupied decreased dramatically over time.

Medium cod had a higher abundance than large cod but also had a decreasing abundance trend over time. Like large cod, this result held when separating indices of abundance into each of the stock areas. Medium cod were most abundant in the Western Gulf of Maine stock area. The center of gravity for medium cod was typically on the border between the Western Gulf of Maine stock area and the Georges Bank stock area and moved slightly offshore over time. The effective area occupied decreased over time.

Small cod had high variability through the time series and seemed to have a jump in recruitment at around 2003. There is no clear trend in small cod abundance over time, though there may have been a slight increasing trend since 2003. Small cod are most abundant in the Southern New England stock area. The center of gravity for small cod was typically in either Southern New England or Western Gulf of Maine waters around Cape Cod, though occasional strong abundance years for coastal Maine pulled the center of gravity dramatically northwards. There is no clear trend for changes in the effective area occupied over time.

**4.2 Fall Index**

Large cod usually had the lowest abundance within the study area of all three size classes, and abundance for this group decreased over time. This result held for indices calculated within each of the four stock areas as well. Large cod were most abundant in the Georges Bank stock area. The center of gravity for large cod tended to be between the Georges Bank and Western Gulf of Maine stock areas and shifted slightly north over the time series. The effective area occupied decreased dramatically over time.

Medium cod had the highest fall abundance of all size classes but also had a decreasing abundance trend over time. Similar to large cod, this result held when separating indices of abundance into each of the stock areas. Medium cod were most abundant in the Western Gulf of Maine stock area. The center of gravity for medium cod was typically on the border between the Western Gulf of Maine stock area and the Georges Bank stock area and moved slightly north over time. The effective area occupied decreased over time.

Unlike the spring indices, small cod did not have high variation in the fall indices. Small cod abundance had a decreasing trend throughout the time but had a rapid fall in abundance in the Southern New England and Western Gulf of Maine stock areas starting around 2010. The center of gravity for small cod was in the Western Gulf of Maine stock area, and there is no clear trend in movement over time. There is also no clear trend for changes in the effective area occupied over time.

**4.3 Habitat associations**

After modeling, VAST extrapolation grid cells were stratified into hard, mixed, and soft bottom types using k-means clustering. Soft-bottom grid cells most likely contained only mud or sand, mixed-bottom cells contained similar likelihoods of mud, sand, and gravel, and hard-bottom grid cells likely contained cobble. The resulting map of sediment “hardness” was plotted with the aggregate spatial density of each cod size class for the spring and fall time series.

Small cod were highly concentrated in nearshore waters around Martha’s Vineyard and Narragansett Bay during the spring season, and more concentrated in nearshore waters around Boston Harbor in the fall. They were not strongly associated with any sediment type, though areas of high abundance in the fall were typically in areas of mixed sediment. Medium cod were more generally spread throughout the Gulf of Maine and densest in areas of mixed sediment type. Large cod were highly dense in much smaller spatial areas. In the spring, this density was concentrated at the eastern end of Georges Bank and within areas of mixed sediment type. In the fall, large cod density was highest in the waters around the Westen Gulf of Maine closed area and within habitats of either mixed or hard sediment type.

**4.4 Model diagnostics**

The effect of anisotropy was stronger in the first linear predictor than the second, meaning that the probability of encountering cod was similar for longer distances along the northeast-to-southwest axis than the abundance of cod along the same axis.

Residual plots did not indicate any violation of assumptions in the construction or implementation of the model. Mapping residuals within the model spatial domain did not highlight any spatial area as having a consistently poor fit.

**5 Discussion**

Currently, groundfish population assessments rely heavily on data gathered with bottom trawl surveys. Despite evidence of increased cod abundance in areas with complex bottom habitats, locations with large-grain sediments or high rugosity are avoided or sampled at low frequency with bottom trawls due to the risks of damaging equipment. This is a major point of contention for fishing industry members, who believe that limiting information from complex habitats will not accurately reflect cod spatial distribution or abundance (Grabowski et al. 2020). Industry members instead support sampling across all habitat types and utilizing dynamic stratification, in which areas of similar habitat characteristics and likelihood of encountering cod are grouped into strata for sampling and later inclusion in assessment efforts. These strata cannot be built without accurate information on cod spatial density for all habitats within their spatial range.

VAST models can provide a flexible but robust framework to better assess groundfish populations across all habitat types within their spatial ranges. This is, of course, reliant on the collection of survey data in areas typically not well sampled by bottom trawls and by high-quality environmental and habitat data as density covariates. The model of cod spatial density created in this project utilized observation data from a suite of gear types and survey platforms, which bridged some of the data gaps inherent to models built with only bottom trawl survey data. The VAST modeling framework allowed for the use of density covariates to interpolate cod spatial density in non-sampled areas with known habitat and environmental characteristics. Further, VAST allowed for the estimation of spatial, temporal, and spatiotemporal correlation of cod abundance, as well as the inclusion of vessel effects, to facilitate the combination of observation data from multiple sources with varied protocols. This modeling process may be more favorable to industry stakeholders than models built with only bottom trawl observation data.

VAST models highlighted the variable spatial density of cod size classes across the four stock areas within the model spatial domain. There was a clear north-south directional gradient of abundance linked to size, where small cod were most abundant furthest south among the size classes and large cod were most abundant furthest north among the size classes. Further, VAST results highlighted the importance of relatively small areas within the stock areas to the size classes of cod. For example, the importance of Georges Bank to the large size class was highlighted; in the spring season, large cod abundance was highest in Georges Bank, driven by high spatial density at its eastern edge. For small cod, areas of high spring spatial density included the nearshore waters at the southwest edge of Martha’s Vineyard.

Cod populations have continued to decline regardless of spatial area closures and massive reductions in fishing pressure. This trend is echoed in model results for all age classes in the fall time series, and all but small cod in the spring time series. The model does not support high emigration out of the model spatial domain as the cause of this population decline; stock centers of gravity for all size classes were typically well within the spatial bounds of the model. This indicates that factors other than fishing are playing a large role in preventing the recovery of the cod population. It is possible that reductions in fishing and spatial area closures are not protecting juveniles, which may be more important to cod population growth than adult survival and fecundity (Wright 2014). VAST results have shown variable distribution of cod by size class, with smaller fish preferring more southern, inshore waters with variable sediment types. Characterization of bottom habitat and subsequent modeling of length-specific habitat associations could help address this uncertainty and lead to more effective protective measures.

Stock centers of gravity and the effective area occupied are variable with cod size but generally indicate a northward and offshore shift and contraction in spatial distribution. Range shifts towards more northerly and deeper water have been commonly seen in North American marine species (Fredston et al. 2021). For cod, this range shift may be related to warming bottom temperatures in areas historically occupied by cod, particularly in the inshore and southern areas of their spatial range. As cod populations move, it will be important to quantify the possible reduction in high-suitability habitats. This will require robust models of cod habitat associations built on cod observation data and high-quality habitat data throughout the cod spatial range.